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A KEY TO THE COLOMBIAN SPECIES OF HOLOSTIPOUS LEJEUNEACEAE (HEPATICAE)

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Resumen

Se provee la sinopsis y la clave, con énfasis en carácteres vegetativos, para 72 especies (en 34 géneros) de lejeuneaceae con anfigastros enteros para Colombia y regiones aledañas. También se suministra una breve información sobre la ecología y distribución altitudinal de las especies en Colombia. A la lista de Hepáticas de Colombia (Gradstein y Hekking 1979) se agregan 10 especies de la flora de Colombia, así mismo, 36 nombres de especies colombianas pasan a ser sinónimas.

Abstract

A synopsis and key emphasizing vegetative characters are provided for 72 species (in 34 genera) of Lejeuneaceae with undivided underleaves, recorded from Colombia and neighbouring areas. A brief statement on the altitudinal distribution and on the ecology of the species in Colombia is also provided. The checklist of the Hepaticae of Colombia (Gradstein & Hekking 1979) is updated; 10 species are added to the Colombian flora and 36 species names recorded from Colombia have fallen into synonymy.

Introduction

The Lejeuneaceae include hundreds of species in about 80 genera world-wide and are the largest family of the Hepaticae. They are the dominant group of bryophytes in tropical lowland rain forest and usually grow on bark of trees or shrubs, or on living leaves. The species vary considerably in size: in some genera (*Aphanolejeunea, Cololejeunea, Microlejeunea*) they are very tiny and only a few millimeters long, in others (*Bryopteris, Thysananthus, Symbiezidium*) they are rather robust and up to a decimeter long or more. The taxonomy of the Lejeuneaceae is usually considered very difficult because of the very large number of species and genera and because of the extensive literature which is not easily accessible to the nonspecialist. Although a number of revisions and monographs have appeared in recent years, there is a lack of good keys, descriptions, and illustrations. In particular, there is a need for keys based on vegetative characters as specimens are often collectec without mature perianths or androecía. The present paper is aimed at filling this gap in the literature by providing a key, based mainly on vegetative characters, for the Colombian species of Lejeuneaceae with entire underleaves. By their underleaves, Lejeuneaceae can be divided into three groups: the "Holostipae", characterized by the presence of undivided underleaves, the "Schizostipae", characterized by bifid underleaves, and the "Astipae", which lack underleaves. The Holostipae comprise the more robust and often brownish or blackish pigmented species, whereas the Schizostipae and the Astipae contain all the tiny, pale green taxa, including many epiphylls. The taxonomy of the schizostipous and astipous Lejeuneaceae is much more poorly known than that of the holostipous Lejeuneaceae, and is in need of much work. A key to these groups would be urgently needed, yet would be very difficult to make in view of our poor knowledge of the species.

The Key includes all 60 holostipous species (in 32 genera) hitherto recorded from Colombia as well as 12 species recorded from neighbouring areas. The latter species may be expected to occur in Colombia as well. The Key has been prepared in the course of the author's monographic work on the Lejeuneaceae for FLORA NEOTROPICA (Gradstein 1987, 1990, in prep.).

The Key emphasizes vegetative characters to facilitate the identification of sterile material. As much as possible information is included on the altitudinal distribution and ecology of the

species. The data on distribution and ecology are based on the literature, on label data of herbarium specimens, as well as on the author's unpublished field observations. The altitudinal distribution is given according to the altitudinal belts of Prance (1989) and Frahm & Gradstein (in press), as follows *lowlands*, up to 300-500 m; *submontane*, up to 1000-1400 m; *lower montane* (= subandean), up to 1800-2400 m; *upper montane* (= andean), up to 3000-3400 m; *subalpine* (= high andean/subpáramo), up to the three line; *alpine* (= páramo). Species which occur throughout the lower and upper montane belts are *montane* species.

Synopsis of Colombian species of holostipous Lejeuneaceae

The last overview of holostipous Lejeuneaceae from Colombia was by Gradstein & Hekking (1979). Their list included many names which are now considered synonyms (see list of Synonyms at the end of this paper).

The species and genera of holostipous Lejeuneaceae currently known from Colombia are listed below in alphabetical sequence; they belong to the subfamilies Ptychanthoideae and Lejeuneoideae. Species new to Colombia (not included in the catalogue by Gradstein & Hekking 1979) are in **bold face.** Species not yet recorded from Colombia but included in the Key are in roman. Publications which provide full descriptions of the species are referred to in brackets.

PTYCHANTHOIDEAE

Acanthocoleus aberrans (Kruijt 1988).
Acrolejeunea emergens, A. torulosa (Gradstein 1975).
Archilejeunea auberiana, A. crispistipula, *A* fuscescens, *A. parviflora, A. porelloides* (Gradstein & Buskes 1985).
Blepharolejeunea incongrua, B saccata, O. securifolia (van Slageren & Kruijt 1985).
Brachiolejeunea laxifolia, B. leiboldiana, B phyllorhiza (van Slageren 1985, Kruijt & Gradstein 1986).
Bryopteris diffusa, B. filicina (Stotler & Crandall-Stotler 1974).
Caudalejeunea lehmanniana (Schuster 1980).
Dicranolejeunea axillaris (Kruijt 1988).
Frullanoides corticalis, F. densifolia, F. liebmanniana, F. tristis (van Slageren 1985).
Lindigianthus cipaconeus (Kruijt & Gradstein 1985).
Lopholejeunea nigricans, L. subfusca (Schuster 1980, Gradstein in prep.).
Marchesinia brachiata, M. robusta (Spruce 1884).
Mastigolejeunea auriculata (inclus. subsp. *plicatiflora*) (Schuster 1980, Gradstein in prep.).
Neurolejeunea breutelii, N. seminervis (Spruce 1884, Schuster 1980).
Odontolejeunea decemdentata, O. lunulata, O rhomalea (Teeuwen 1989).
Schiffneriolejeunea amazónica, S. polycarpa (Evans 1908, Gradstein 1985a).
Spruceanthus theobromae (Spruce 1884, Gradstein 1985a).
Stictolejeunea balfourii, S. squamata (Gradstein 1985b).
Symbiezidium barbiflorum, S. dentatum, S. transversale (Gradstein & van Beek 1985).
Thysananthus amazónica, T. pterobryoides (Fulford 1941).
Verdoornianthus griffinii (Gradstein 1978).

LEJEUNEOIDEAE

Amphilejeunea catinulifera, A. Patellifera, ***A. viridissima*** (Schuster 1986).
Anoplolejeunea conferta (Evans 1908).
Aureolejeunea ***aurífera, fulva,*** *A. paramicola, A.* ***quinquecarinata*** (Schuster 1986, 1987).
Ceratolejeunea globulífera, C. grandiloba (Grolle 1987).
Cheilolejeunea fragrantissima (Spruce 1884).
Cyclolejeunea convexistipa (Evans 1904, Grolle 1984).
Cyrtolejeunea holostipa, C. saccatiloba, C. venezuelana (Schuster 1970, 1978, Gradstein & Buskes 1985).
Lejeunea reflexistipula (Spruce 1884).
Lepidolejeunea eluta, ***spongia*** (Piippo 1986).
Leucolejeunea unciloba, L. xanthocarpa (Schuster 1980).
Luteolejeunea herzogii (Piippo 1986).
Omphalanthus filiformis, O. jackii, O. ovalis, O. platycoleus, wallisii (Gradstein et al. 1981, Gradstein & Buskes 1985).
Taxilejeunea sulphurea (Spruce 1884).

Key to Colombian species of holostipous Lejeuneaceae

1a. Leaf margin toothed, at least near apex **2**
1b. Leaf margin entire **17**
2a. Stems thin and fragile, pale colored; ventral stem surface only 2-3 epidermis cells wide (above or below the underleaf insertion area) **3**
2b. Stems rather thick and rigid, usually brown; ventral stem surface 4 or more cells wide **12**
3a. Underleaves toothed. ***Odontolejeunea*** (Spruce) Schiffn. **4**

3b. Underleaves entire **5**

4a. Leaf margins revoluted when dry; leaf cells orientated in transverse rows extending from dorsal to ventral leaf margin; lobule with (3-)4-6 teeth. On leaves or twigs in submontane and montane rain forest (rarely lowlands) ..... ***O. rhomalea*** (Spruce) Steph.

4b. Leaf margins plane, involuted or irregularly crisped when dry, not revoluted; leaf cells orientated in longitudinal rows (as usual in Leujeneaceae) extending from leaf base to apex; lobule with 2-4 teeth. On leaves or bark in lowland and montane forest ..... ***O. lunulata*** (Web.) Schiffn.

5a. Ocelli present in leaves: scattered, in a short row or 1-2 near leaf base **6**

5b. Ocelli lacking **8**

6a. Plants pale-green; large rounded gemmae often present on leaf margins; perianth strongly toothed, without horns. On leaves, bark or rock in lowland and montane forest ..... ***Cyclolejeunea convexistipa*** (Lehm. & Lindenb.) Evans

6b. Plants brown; gemmae lacking; perianth without teeth, the apex with four horn-like extensions ..... ***Ceratolejeunea*** (Spruce) Schiffn. (subg. *Ceratophora*) **7**

7a. Plants ca. 2 mm wide; underleaves 3-4x stem width. Epiphyte in montane and subalpine rain forest ..... ***C. grandiloba*** Jack & Steph.

7b. Plants smaller, 1-1.5 mm wide; underleaves 2x stem width. Epiphyte in lower montane rain forest ..... ***C. globulifera*** Herz.

8a. Underleaves very large, 6-10x stem width, at apex short bifid or notched; lobule minute; perianths without keels, on short lateral, innovating branches. Widespread epiphyte of lower montane elevations ..... ***Taxilejeunea sulphurea*** (Lehm. & Lindenb.) Schiffn.

8b. Underleaves smaller, apex undivided **9**

9a. Leaves with (5-)7-25 teeth; underleaves often producing a large, circular disc formed by coalesced rhizoids; plants often epiphyllous ..... ***Odontolejeunea*** (Spruce) Schiffn. **10**

9b. Leaves with 1-7 teeth; rhizoid disc lacking; not epiphyllous **11**

10a. Underleaf bases with sharp auricles; lobule with 2-4 teeth. On leaves or bark in lowland and montane forest ..... ***O. lunulata*** (Web.) Schiffn.

10b. Underleaf bases cuneate, without sharp auricles; lobule with 0-1(-2) teeth or reduced. On leaves or twigs in lowland and lower montane rain forest ..... ***O. decemdentata*** (Spruce) Steph.

11a. Lobule at least ½x leaf length; underleaf insertion straight; leaves strongly falcate. On bark at lower montane elevations, not yet recorded from Colombia .. ***Blepharolejeunea saccata*** (Steph.) van Slag. & Kruijt

11b. Lobule smaller, up to ⅓x leaf length, sometimes reduced; underleaf insertion arched; leaves not or slightly falcate **36**

12a. Underleaves toothed **13**

12b. Underleaves entire **16**

13a. Stems ± creeping, branching sparse or dichotomous; underleaf apex recurved, rounded; line of insertion of the underleaf very deeply arched (depth of the insertion about half as long as the total underleaf); lobule with 3-4 small teeth; perianth flat, with 2 innovations. On bark or rock at submontane or lower montane elevations ..... ***Marchesinia robusta*** (Mitt.) Schiffn.

13b. Stems erect or pendent, pinnately branched or dichotomous; underleaf apex plane, rounded, truncate or emarginate; underleaf insertion line straight or slightly curved; lobule with one tooth or with several very large teeth **14**

14a. Underleaf apex emarginate; leaf cells isodiametric, the cell walls uniformly thickened, trigones lacking; lobule with a long, curved tooth; perianth with 2 innovations; plants densely pinnate, dendroid. Along the Pacific coast (Chocó) and locally at the foot of the Andes, in submontane rain forest .. ***Thysananthus pterobryoides*** (Spruce) Schiffn.

14b. Underleaf apex rounded to truncate; leaf cells distinctly longer than wide, the walls with small trigones and intermediate thickenings; lobule with a small tooth or with several very large teeth; perianth on a short lateral branch without innovations; plants pinnate or dichotomous. Common in submontane and lower montane forests ..... ***Bryopteris*** (Nees) Lindenb. **15**

15a. Branching dichotomous; lobule with several very large teeth ..... ***B. diffusa*** (Sw.) Nees

15b. Branching ± pinnate; lobule with 1 small tooth .... ***B. filicina*** (Sw.) Nees

16a. Leaf apex broadly recurved; cell walls colorless; epidermal cells thin-walled; lobule ca. ⅓x leaf length. Above 2000 m. on shrubs, tree ferns (*Blechnum*) and over litter in humid, high montane environments ..... ***Lindigianthus cipaconeus*** (Gott.) Kruijt & Gradst.

16b. Leaf apex plane, cell walls often with blackish pigmentation; epidermal cells thickened; lobule smaller; usually below 2500 m **17**

17a. Lobule plane, with 2-4 teeth spaced regularly along the free margin; perianth smooth, on an elongated shoot and with 2 long innovations; epi dermal cells scarcely larger than inner stem cells (stem cross section). On bark or rock at submontane and lower montane elevations ..... ***Marchesinia brachiata*** (Sw.) Schiffn.

17b. Lobule inflated-rounded, teeth lacking or obscure; perianth ciliate-laciniate, on a very short branch and with 1 short innovation; epidermal cells distinctly larger than inner cells. Along the Pacific coast (Chocó), on bark in lowland rain forest ..... ***Symbiezidium dentatum*** Herz. (=*S. transversale* subsp. *dentatum* (Herz.) Gradst. & van Beek)

18a. Leaves with ocelli **19**

18b. Ocelli lacking **23**

19a. Ocelli arranged in a row, forming a vitta (= nerve) of 7-22 cells long; lobule with a long, 3-5 cells long tooth. In the canopy of lowland, Amazonian forest

and in bushes; not yet recorded from Colombia ... . ***Neurolejeunea seminervis*** (Spruce) Schiffn.

19b. Ocelli scattered through the leaf; lobule with a short tooth **20**

20a. Ventral stem surface 4 or more cells wide; *Frullania-type* branching present or lacking ..... ***Stictolejeunea*** (Spruce) Schiffn. 20 *(Lepidolejeunea eluta* (Nees) Schust. might also key out here. This species has underleaves shallowly bifid however, up to 0, 1-0,2 of their length; furthermore, lobules are rather large, ca. ⅓x lobe length, the leaf apex is acute and the cells are very thin-walled).

20b. Ventral stem surface 2 cells wide; *Frullania-type* branching lacking **22**

21a. Underleaves wider than long, (3)4-10 x stem width; vegetative branches always of the *Frullania-type;* plants 1,2-2,5 mm wide, creeping or pendent, when pendent regularly (bi-)pinnate, when creeping irregularly branched. Common epiphyte in lowland and lower montane rain forests .... ***S. squamata*** (Willd. ex Web.) Schiffn.

21b. Underleaves suborbicular, 2-3 x stem width; vegetative branches of the *Lejeunea-type* (rarely a *Frullania-type* branch present); plants smaller, 1-1,3 mm wide, creeping, irregularly branched. Rare species in the shaded understory of lowland rain forest (on tree bases, roots, etc.), usually near running water ..... ***S. balfourii***(Mitt.) E.W. Jones

22a. Stem fragile, the cell walls thin; lobule "normal" in position (opening oriented toward leaf apex), the keel forming an angle of 50-90° with the stem; ocelli ∓ equal in size to ordinary leaf cells or smaller, rather inconspicuous; trigones lacking. In the canopy of montane rain forest or on shrubs .... ***Lepidolejeunea spongia*** (Spruce) B. Thiers

22b. Stem rigid, the walls thickened; lobule curved downwards, the keel forming an angle of 120-140° with the stem; ocelli mostly larger than leaf cells; trigones well-developed. Along the Pacific coast (Chocó) in lowland and lower montane forest .... ***Luteolejeunea herzogii*** (Buchloh) Piippo

23a. Leaf cells more or less longer than wide, with cordate trigones having 2 side convex and 1 side concave; leaves when dry convoluted (weakly so in Caudalejeunea, couplet 38) **23**

23b. Leaf cells isodiametric (elongated in *Neurolejeunea,* couplet 41, and *Spruceanthus,* couplet 54), the trigones various but not cordate; leaves when dry spreading, curved down or folded but not convoluted **41**

24a. Lobule with 3-10 teeth (teeth sometimes inflexed and inconspicuous) **25**

24b. Lobule with 1-2 teeth **31**

25a. Epidermis cells ± thick-walled, surrounding a thin-walled medulla; lobule with 3-4 teeth; perianth with 3 keels and 2 innovations; dorsal stem surface with a 1-4 cells high lamellate paraphyllium. Common at high elevations (2000-3500 m.) on bark or rock .. ***Brachiolejeunea laxifolia*** (Tayl.) Schiffn.

25b. Epidermis cells ± thin-walled (especially dorsally), surrounding a thicker-walled medulla; lobule with 3-10 teeth; perianth with 5-10 keels or plicae, with or without innovations **26**

26a. Plants usually black; innovations present; flagelliform shoots lacking. Lowlands and montane .... ***Frullanoides*** Raddi **27**

26b. Plants yellowish-brown; innovations lacking; flagelliform shoots common, producing small caducous leaves. Lowlands only, rather xerophytic, in savanna, scrub, and in the canopy and at the edges of rain forest .... ***Acrolejeunea*** (Spruce) Schiffn. **30**

27a. Leaf apex acute-apiculate or obtuse; underleaves distinctly auriculate (auricles 0.1-0.3 mm long, appressed to the stem), the insertion line deeply arched. Common on bark or rock at montane elevations ..... ***F. densifolia*** Raddi

27b. Leaf apex broadly rounded; underleaves not or weakly auriculate (auricles less than 0.1 mm long), the insertion line straight or curved **28**

28a. Underleaves not auriculate; plants 1- 1.5 mm wide; lobule teeth with 4-6 teeth, the small first tooth situated in the sinus at the junction with the ventral leaf margin; dioicous; male bracts hypostatic. Lowland epiphyte, along the coast .... ***F. corticalis***(Lehm. & Lindenb.) van Slag.

28b. Underleaves weakly auriculate; plants 1.5-3 mm wide; lobule with 3-9 teeth, no tooth in the sinus; male bracts epistatic. Submontane and montane **29**

29a. Lobule with 3-5 rather large, triangular teeth; dioicous ***F. liebmanniana*** (Gott. & Lindenb.) van Slag.

29b. Lobule with 5-9 narrow, sharp teeth; paroicous ..... ***F. tristis*** (Steph.) van Slag.

30a. Lobule with 3-4 large triangular teeth, the first tooth erect ..... ***Acrolejeunea emergens*** (Mitt.) Steph.

30b. Lobule with 5-8 teeth, the first tooth usually outwardly curved .... ***A. torulosa*** (Lehm. & Lindenb.) Schiffn.

31a. Ventral epidermal cells not larger than inner stem cells (cross section). Plants of lower elevations (below 1500 m.) **32**

31b. Ventral epidermis cells larger than inner cells. High or low elevations **35**

32a. Lobule with (1-)2 teeth; cell walls colorless, plants turning brown; perianth with 4-5 keels, innovations lacking ..... ***Schiffneriolejeunea*** Verd. 32

32b. Lobule with 0-1 teeth; cell walls of older leaves normally with dark pigmentation, plants turning black; perianth with 3(-8) keels, innovations present **34**

33a. Lobule ovate, ⅓-⅔x leaf length; perianth with 2 short, broadly rounded ventral keels; lobule of inner female bract shorter than lobe. In submontane forest (canopy) and bushes, rare in Colombia .... ***S. polycarpa*** (Nees) Gradst.

33b. Lobule narrow rectangular, ½-⅗x lobe length; perianth with 2 long, sharp ventral keels; lobule of inner female bract as long as the lobe. In lowland savannas, bushes and tree crowns in Amazonia,

not yet recorded from Colombia ..... ***S. amazónica*** Gradst.

34a. Leaf apex rounded or obtuse; underleaves truncate; female bracts entire. Forming mats on bark in the canopy and at the edges of lowland and submontane forest and in bushes, up to 1500 m ..... ***Mastigolejeunea auriculata*** (Wils.) Schiffn. (A perianth with more than 3 keels is characteristic for *M. auriculata* subsp. *plicatiflora* (Spruce) Gradst.; this subspecies is common in Amazonia and should also occur in Colombia)

34b. Leaf apex sharply acute-apiculate; underleaf apex emarginate; female bracts toothed. Rather long, often pendent plants in lowland Amazonian rain forest, forming small festoons on branches and twigs ..... ***Thysananthus amazonicus*** (Spruce) Schiffn.

35a. Lobule never reduced, the apex sharply truncate, with 2 dissimilar teeth: the second tooth large, situated at lobule angle, sharp, pointing outwards, the first tooth smaller, incurved and blunt. High montane, 2000-4000 m., on bark or rock in exposed habitats ..... ***Blepharolejeunea*** S. Arn. 35

35b. Lobule reduced or well-developed, the apex rounded or oblique, the teeth equal or the first tooth larger than the second tooth. Lowland or montane **37**

36a. Lobule bordered by enlarged margin cells; perianth up to 1 mm long, the lateral keels sharp, entire or ciliate; lobule of female bract small, less than ⅓x lobe length ..... ***B. incongrua*** (lindben. & Gott.) van Slag. & Kruijt

36b. Lobule margin cells not enlarged; perianth over 1 mm long, the lateral keels broadly rounded, entire; lobule of female bract larger, ½-⅔x lobe length. Above 3000 m. only ..... ***B. securifolia*** (Spruce) Schust.

37a. Ventral stem surface 2 epidermis cells wide (outside leaf insertion area) **38**

37b. Ventral stem surface 4 epidermis cells wide . **39**

38a. Branches predominantly *Frullania-type,* plants often pendent when growing on bark; epidermis cells thinwalled, bulging outwards; female bracteole toothed. Common at submontane and montane elevations, on bark, rock or soil in open habitats . ..... ***Dicranolejeunea axillaris*** (Nees & Mont.) Schiffn.

38b. Branches predominantly *Lejeunea-type,* plants always creeping; epidermis cells ± thick-walled, not bulging outwards (Stem surface smooth); female bracteole entire. Submontane and lower montane, on bark or rock, in open habitats and tree crowns . ..... ***Acanthocoleus aberrans*** (Lindenb. & Gott.) Kruijt

39a. Leaves not squarrose when moist; *Frullania-type*-branches lacking; intermediate thickenings 1-3 per cell wall; perianth with 4-5 keels, lacking innovations. In lowlands on leaves or twigs in exposed habitats ..... ***Caudalejeunea lehmanniana*** (Gott.) Evans

39b. Leaves squarrose when moist, when dry strongly convoluted; *Frullania-type* branches usually present; cell walls with 0-1 intermediate thickenings; perianth with 3 keels and with innovations. Submontane and lower montane (300-2000 m.), on bark or rock in exposed, rather dry habitats .... **Brachiolejeunea**(Spruce) Schiffn. 40

40a. Stem dorsally with a 1 cell high lamellate paraphyllium; lateral perianth keels rounded, smooth; dioicous? (males unknown) ..... ***B. leiboldiana*** (Gott. & Lindenb.) Schiffn.

40b. Paraphyllium lacking; lateral perianth keels sharp, dentate-ciliate or smooth; autoicous, male bracts on short-specialized branches .... ***B. phyllorhiza*** (Nees) Kruijt & Gradst.

41a. Ventral stem surface 4 or more cells wide (outside underleaf insertion area) **42**

41b. Ventral stem surface 2 cells wide **66**

42a. Leaf cells small, ca. 10-20 μm, without or with obscure trigones; lobule usually conspicuously darker than lobe, bottle-shaped, with a long, sharp tooth (usually incurved and invisible without dissection); perianth keels at apex expanded into auricles; plants small, less than 1,5 mm wide, usually blanckish. Lowlands to 3000 m., on bark or rock . ..... ***Neurolejeunea breutelii*** (Gott.) Evans

42b. Leaf cells larger, usually with distinct trigones; lobule not conspicuously darker than lobe; perianth keels not expanded into auricles **43**

43a. Lobule with 204 teeth **44**

43b. Lobule with only one tooth or tooth lacking ... **48**

44a. Lobule well-developed, the apex truncate, with 2 dissimilar teeth, the second tooth larger than the first tooth: first tooth incurved and blunt, second tooth situated at lobule angle, long and sharp . **45**

44b. Lobule reduced or well-developed, the apex rounded oblique, the teeth identical or the first tooth larger than the second tooth **46**

45a. Plants whitish to pale grayish-green; lobule about 2x longer than wide; *Frullania-type* branches lacking. Lower montane, up to 2500 m .. ***Leucolejeunea unciloba*** (Lindenb.) Evans **48**

45b. Plants darker, greenish-brown to dark brown; lobule 1-1.5x longer than wide; *Frullania-type* branches present. Montane-alpine, 2000-4000 m .... ***Blepharolejeunea*** S. Arn. **35**

46a. Lobules sometimes reduced, when well-developed rectangular, with 2 teeth at apex; underleaves 3-4,5 x stem stem width, the insertion line straight; plants 1-2 mm wide, greenish to yellowish-brown; perianth infalted, with 2 ventral keels. Lowland and submontane, not yet recorded from Colombia (0-1000 m) .... ***Archilejeunea auberiana*** (Mont.) Evans (× ***A. parviflora*** var. *florentissima* (Spruce) Gradst. & Buskes)

46b. Lobules never reduced, ovate-trapezoidal, with 2-4 teeth regularly spaced along the free margin; underleaves 4-10 x stem, the line of insertion deeply arched; plants rather robust, usually more than 2 mm wide, often blackish; perianth flattened, wit-

hout ventral keels. Submontane and montane, lacking in lowlands, on bark or rock ..... ***Marchesinia*** S. Gray 47

47a. Underleaf margin entire ..... ***M. brachiata*** (Sw.) Schiffn.

47b. Underleaf margin dentate ..... ***M. robusta*** (Mitt.) Schiffn.

48a. Plants whitish or pale yellowish, growing appressed. Submontane-lower montane, on bark or rock in rather exposed habitats ..... ***Lecolejeunea.***Evans 49

48b. Plants darker, green, brown or blackish. Lowlands to alpine elavations, growing appressed or free from the substrate in sheltered or exposed habitats **50**

49a. Ventral leaf margin strongly involuted; lobule tooth 1-4 cells long ..... ***L. xanthocarpa.*** (Lehm. & Lindenb.) Evans

49b. Ventral leaf margin plane or slightly upcurved; lobule tooth 3-7 cells long ..... ***L. unciloba.*** (Lindenb.) Evans

50a. Epidermis cells larger than inner stem cells (cross section); plants often blackish; perianth keels dentate-laciniate **51**

50b. Epidermis cells not larger than inner cells; plants not blackish (except sometimes *Archilej. Parviflora,* couplet 54); perianth keels smooth or denticulate **54**

51a. Plants 2-5 mm wide; underleaves very large, 5-10x stem width; lobule always small, less than ¼x leaf length, strongly infalted; perianth on a very short shoot (appearing lateral on the stem), with one short innovation. Lowlands to montane, up to ca. 2500 m ..... ***Symbiezidium Trevis*** **52**

51b. Plants smaller, 1-2 mm wide; underleaves 2-5x stem width; lobule ⅓-½x leaf length or reduced, inflated or flattenede; perianth on an elongated shoot, usually without innovations. Lowlands to lower montane, up to ca. 2000 m ..... ***Lopholeujenea*** (Spruce) Schiffn. 53

52a. Plants 2-2.5(-3) mm wide; ventral surface of perianth rough due to spines or laciniae, which are distributed randomly as well as (sometimes) in 1-2 rows. Sealevel to 2500 m., on bark in forests .... ***S. barbiflorum*** (Gott.) Evans

52b. Plants 2.5-5 mm wide; ventral surface of perianth entirely smooth or with a few spines and laciniae arranged in 1-2 rows (never randomly distributed). Distribution as *S. barbiflorum* but usually at lower altitudes (not found above 1700 m.) ..... ***S. transversale*** (Sw.) Trevis.

53a. Leaf apex acute to rounded; perianth long, distinctly exserted, weakly toothed-laciniate only; apex of lobule acute, not connate with leaf surface. Plants growing in loose mats in rather moist, shaded habitats, usually submontane-lower montane ..... ***L. muelleriana*** (Gott.) Schiffn.

53b. Leaf apex rounded; perianth short, hidden behind a very large bracteole, with very large laciniae emerging beyond the bracteole; apex of lobule often truncate and connate with the lobe surface across 2-3 cells. Plants growing in dense, appressed mats in exposed, often rather dry habitats, usually lowland-submontane ..... ***L. subfusca*** (Nees) Schiffn.

54a. Leaf cells with many intermediate thickenings (1-3 per cell), trigones radiate; hyaline papilla proximal of the apical tooth of the lobule; male bracteoles present throughout the male spike. In lowland forests **55**

54b. Leaf cells without or with very few intermediate thickenings (0-1 per cell), trigones usually large and bulging, not radiate; hyaline papilla situated in a small sinus (or on the inner lobule surface) distal of the apical tooth; male bracteoles limited to the base of the spike. In mountain forests and páramos **60**

55a. All or at least some lobules poorly developed; innovations *lejeuneoid* (first leaf at the base of the innovation is a lateral leaf) **56**

55b. All lobules well-developed, never tending to become reduced; innovations *pycnolejeuneoid* (first leaf at the base of the innovation is an underleaf) or lacking **57**

56a. Leaf cells distinctly elongated, about 2x longer than wide; plants robust, ca. 3 mm wide; ventral stem surface ca. 12 cells wide. Endemic to the Pacific coast of Ecuador, not yet recorded from Colombia ..... ***Spruceanthus theobromae*** (Spruce) Gradst.

56b. Leaf cells isodiametric; plants smaller, 1-2 mm wide; ventral stem surface 4-6 cells wide. On bark or rock in moist lowland and submontane forests (0-1500 m.), always in shaded habitats ..... ***Archilejeunea parviflora*** (Nees) Gradst.

57a. Plants glossy brown; leaves when moist widely spreading, not squarrose; free margin of the lobule plane; innovations present; dioicous. Epiphytes in Amazonian lowland forests ..... ***Archilejeunea*** (Spruce) Schiffn. (subgen. *Archilej.*) 57

57b. Plants dull brown; leaves when moist suberect, not spreading widely, ± squarrose; lobule rectangular, the free margin partly incurved; innovations lacking; autoicous. Rare canopy epiphyte of Amazonian lowland rain forest, not yet recorded from Colombia ..... ***Verdoornianthus griffinii*** Gradst.

58a. Underleaf margins undulate; ventral leaf margin auriculate at the junction wit the keel. Epiphyte in periodically inundated Amazonian forest, not re corded from Colombia ..... ***A. crispistipula*** (Spruce) Steph.

58b. Underleaf margins plane; ventral leaf margin not auriculate **59**

59a. Plants robust, 2-3 mm wide; underleaves longer than wide to orbicular; lobule apex triangular, lacking a distinct tooth. Epiphyte in Amazonian rain forest and scrub . ***A. porelloides*** (Spruce) Schiffn.

59b. Plants smaller, 1-2 mm wide; underleaves wider than long or (in small plants) orbicular; lobule apex with 1 tooth. Epiphyte in lowland rain forest .....

.... ***A. fuscescens*** (Hampe) Fulf. (× ***A. juliformis*** (Nees) Gradst.

60a. Lobules quadrate-trapezioid, ¼-⅓x lobe length; plants usually pendent, long and little branched, green or pale yellowish-brown in color; perianth with 0-5 keels ..... ***Omphalanthus*** Nees 61

60b. Lobules oblong-rectangular, ⅖-½x lobe length; plants creeping or ± ascending, with short, irregularly branched stems, brownish in color (golden green to light brown in A. fulva, couplet 82); perianth with 3-10 keels . ***Aureolejeunea*** Schust. 63

61a. Leaf apex acute to acuminate' underleaves usually longer than wide' perianth with 5 keels and a long (8 cells) beak **62**

61b. Leaf apex broader, rounded to subobtuse; underleaves wider than long (rarely longer than wide); perianth with or without keels, beak shorter or lacking. Very common in the Andes ..... ***O. filiformis*** *(Sw.) Nees (the perianth of O. filiformis* has no keels; there are two species which are very similar to *O. filiformis* but with different perianths: *O. platycoleus* Herz., which has a 3-4-keeled perianth, and *O. wallisii* (Steph.) Gradst., which has a 5-keeled perianth. The status of the latter two species is not clear).

62a. Leaf apex (sub)acute; underleaves undivided. Lower montane ..... ***O. ovalis*** (Lindenb. & Gott.) Gradst.

62b. Leaf apex acuminate; underleaves short bifid. Rare, not yet recorded from Colombia ... ***O. jackii*** (Steph.) Gradst.

63a. Leaf cells strongly mamillose-papillose; leaf margins crenulate. On bark in páramo ..... ***Aureolejeunea aurífera*** Schust.

63b. Leaf cells ± smooth; leaf margins entire **64**

64a. Perianth pluriplicate, with 3-5 ventral keels; innovations 2; plants rather robust, ascending from the substrate or pendent. Epiphyte, above 3000 m .... .. ***A. paramicola*** (Herz.) Schust. (= *Omphalanthus paramícola* (Herz.) Gradst.

64b. Perianth with only 1-2 ventral keels; innovations 1-2; plants smaller, creeping **65**

65a. Perianth with 5 long, sharp keels, the perianth apex rounded (beak not recessed); plants reddish- to dark-brown. On shrubs at the forest line and in the páramo ..... ***A. quinquecarinata*** Schust.

65b. Perianth near apex with 304 short, broadly rounded keels, the perianth apex emarginate, the beak recessed; plants golden green to light brown. On canopy branches in montane rain forest .... ***A. fulva.*** Schust.

66a. Lobules uniformily swollen and strongly involute, the free margin inrolled 2-3 times. Plants small, pale whitish-green. Common epiphyte in forest canopy and in scrub on twigs, ca. 500-3500 m .... ***Anoplolejeunea conferta*** (Meissn.) Schiffn.

66b. Lobule not or only weakly involute **67**

67a. *Frullania-type* branches present (though sometimes only few); lobule when well-developed with 2 teeth; male bracteoles present throughout the male spike; plants ± brownish pigmented **38**

67b. *Frullania-type* branches entirely lacking; lobules with 1 tooth only; male bracteoles limited to the base of the spike; plants pale green, rarely brownish **68**

68a. Lobule large, ⅖-½x lobe length (or more) **69**

68b. Lobule small, less than ⅓x lobe length **73**

69a. Underleaves large, 4-5x stem width, imbricate; plants rather robust, ca. 1-2 mm wide. Mostly above 2000 m. **69**

69b. Underleaves smaller, 1-2.5x stem width; plants tiny and fragile, 0,5-1 mm wide. Submontane-montane ..... ***Cyrtolejeunea*** Evans 71

70a. Plants brownish; leaf cells with large, bulging trigones, intermediate thickenings lacking; stems rigid, cells strongly thickened .... ***Aureolejeunea*** p.p. 65

70b. Plants pale greenish; leaf cells with small trigones and intermediate thickenings; stem cells ± thin-walled. Epiphyte in montane rain forest (canopy) and bushes ..... ***Amphilejeunea viridissima*** Schust. (two further species, *A. catinulífera* (Spruce) Schust. and *A. patellifera* (Spruce) Schust. from the Andes of Ecuador, have been placed in *Amphilejeunea* (Schuster 1986). The differences among the three species of *Amphilejeunea* are not clear, however, and need further study).

71a. Lobule with a long acuminate tooth; leaves sube-rect; plants very small, *Microlejeunea*-like, ca. 0,5 mm wide. On bark in rain forest ..... ***C. holostipa*** **(Spruce) Evans**

71b. Lobule tooth short or lacking; leaves spreading; plants larger **72**

72a. Lobule tooth short, blunt; underleaves short bifid; dioicous? Venezuela (Tachira), 500 m, not yet recorded from Colombia ... ***C. Venezuelana*** Schust.

72b. Lobule tooth lacking; underleaves entire; autoicous. Not yet recorded from Colombia .... ***C. saccatiloba*** (Steph.) Gradst.

73a. Plants firm, the cells of leaves and underleaves with large trigones; hyaline papilla of the lobule distal of the apical tooth; underleaf apex undivided or notched. Epiphyte of submontane and lower montane elevations .... ***Cheilolejeunea fragrantissima*** (Spruce) Schust.

73b. Plants delicate, the cells thin-walled with very small trigones; hyaline papilla proximal of the apical tooth **74**

74a. Underleaf apex recurved. On bark in lowland and submontane rain forest .... ***Lejeunea reflexistipula*** (Lehm. & Lindenb.) Gott. et al.

74b. Underleaf apex plane **75**

75a. Underleaf apex short bifid or notched (underleaves very large); plants pale green; leaf apex rounded or pointed; ocelli lacking ..... ***Taxilejeunea sulphurea*** **8**

75b. Underleaf apex undivided; plants olive-green to brownish; leaf apex rounded; ocelli present in leaves and underleaves, often rather similar to the green cells in size and shape and therefore obscure in herbarium material .... ***Lepidolejeunea spongia*** **22**

Synonyms

This list includes names of holostipous Lejeuneaceae in the checklist of Colombian liverworts (Gradstein & Hekking 1979), which are now considered synonyms.

Archilejeunea juliformis (Nees) Gradst. =*A. fuscescens* (Hampe) Fulf.
A. leprieurii (Mont.) Schiffn. =*A. parviflora* (Nees) Gradst.
Brachiolejeunea columbica Steph. =*Frullanoides densifolia* Raddi.
B. densifolia (Raddi) Evans =*Frullanoides densifolia* Raddi.
B. nitidiuscula (Gott.) Schiffn. =*Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt.
B. paramicola Herz. =*Aureolejeunea paramicola* (Herz.) Schust.
B. rupestris (Gott.) Steph. =*Frullanoides desinfolia* Raddi *B. succisa* Steph. =*Frullanoides desinfolia* Raddi
B. wrightii Steph. =*Frullanoides tristis* (Steph.) van Slag.
Bryopteris trinitensis (Lehm. & Lindenb.) Lehm. & Lindenb. =*B. filicina* (Sw.) Nees.
B. fruticulosa Tayl. =*B. filicina (Sw) Nees.*
Dicranolejeunea cipaconea (Gott.) Steph. = *Lindigianthus cipaconeus* (Gott.) Kruijt & Gradst.
D. gigantea Steph. =*Frullanoides liebmanniana* (Lindenb. & Gott.) van Slag.
D. grossiloba Steph. =*Odontelejeunea lunulata* (Web.) Schiffn.
D. incongrua (Lindenb. & Gott.) Steph. =*Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt.
D. loxensis (Gott.) Steph. =*Acanthocoleus aberrans* (Gott.) Kruijt.
D. phyllorhiza (Nees) Schiffn. =*Brachiolejeunea phyllorhiza* (Nees) Kruijt & Gradst.
D. tridentata S. Winkler =*D. axillaris* (Nees & Mont.) Schiffn.
Hygrolejeunea patellifera (Spruce) Steph. =*Amphilejeunea patellifera* (Spruce) Schust.
H. reflexistipula (Lehm. & Lindenb.) Steph. =*L. reflexistipula* Lehm. & Lindenb.
Lopholejeunea muelleriana (Gott.) Schiffn. =*L. nigricans* (Lindenb.) Schiffn.
L. saxatilis (Gott. ex Aongstr.) Steph. =*L. nigricans* (Lindenb.) Schiffn.
Marchesinia aguatica Herz. =*M. brachiata* (Sw.) Schiffn.
M. extensa (Steph.) =*M. brachiata* (Sw.) Schiffn.
M. longirostris Herz. =*M. brachiata* (Sw.) Schiffn.
Mastigolejeunea pittieri Steph. =*M. auriculata* (Wils.) Schiffn.
M. plicatiflora (Spruce) Steph. =*M. auriculata* (Wils.) Schiffn. subsp. *plicatiflora* (Spruce) Gradst.
Odontolejeunea calcarea (Spruce) Steph. =*O. lunulata* (Web.) Schiffn.
O. longispica Evans =*O. decemdentata* (Spruce) Steph.
O. obversiloba Herz. =*O. rhomalea* (Spruce) Steph.
O. sieberiana (Gott.) Schiffn. =*O. lunulata* (Web.) Schiffn.
Omphalanthus grandistipulus Steph. =*O. filiformis* (Sw.) Nees.
Pycnolejeunea granatensis Steph. =*Lepidolejeunea eluta* (Nees) Grolle.
Stictolejeunea kunzeana (Gott.) Schiffn. =*S. squamata* (Willd. ex Web.) Schiffn.
Symbiezidium granulatum (Nees) Steph. =*S. transversale* (Sw.) Trevis.
S. subrotundum (Kunth) Trevis. =*S. transversale* (Sw.) Trevis.

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